

# Towards a global classification of excitable reaction–diffusion systems

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Patterns in reaction–diffusion systems near primary bifurcations can be studied locally and classified by means of amplitude equations. This is not possible for excitable reaction–diffusion systems. In this Letter we propose a global classification of two variable excitable reaction–diffusion systems. In particular, we claim that the topology of the underlying two-dimensional homogeneous dynamics can be used to organize the system’s behavior.

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Many dissimilar experimental and model reaction–diffusion systems display similar behavior. This raises the question of whether a classification can be found so that seemingly unrelated systems with similar dynamics can be understood as belonging to the same equivalence class. We argue in this Letter that a global classification is possible for reaction–diffusion systems whenever the underlying homogeneous dynamics can be mapped onto a *planar flow* (i.e., a flow in  $R^2$ ). This classification is done in terms of *model families* [1] that are largely determined by the homogeneous dynamics. In support of our conjecture we analyze experiments done in an open reactor using the FIS (Ferrocyanide–Iodate–Sulfite) reaction [2,3] and two reaction–diffusion models [4,5] that display similar patterns to those of the experiment, even though they are not accurate models of the FIS kinetics. We explain these common behaviors by noting that they all have similar homogeneous dynamics and discuss the main features of their model family.

The classification of system behaviors lies at the heart of dynamical systems theory and here the normal form theorem is one of the main achievements [6]. It states that close to a bifurcation point the dynamics of any sufficiently smooth system can be reduced to a simplified set of equations that is locally topologically equivalent to the full vector field [7]. The normal form approach is local in both phase and parameter space. Thus, classifications based on it provide generic descriptions only when the system is near threshold. For this reason, the patterns that occur in the *excitable systems* that we discuss in this Letter cannot be classified with normal form techniques.

Excitability is a common dynamical behavior that occurs, for example, in the kinetics of neuronal membrane

potentials [8], in semiconductor lasers with feedback [9] and in a variety of chemical reactions [2]. The picture of excitability we use is defined in terms of the spatially uniform dynamics. It assumes the existence of a stable fixed point (a spatially uniform stationary solution) such that perturbations above a threshold result in a large excursion in phase space before the systems decays back to the fixed point. A spatially uniform excitable dynamics can result in wave propagation or in multistability when spatial variations are allowed. In particular this is true when the coupling is diffusive, i.e., for *reaction–diffusion* systems (see e.g. [4]). Since these behaviors arise from a finite perturbation of the spatially uniform steady state, classifications based on local normal forms cannot be used.

We now consider a reaction–diffusion system whose homogeneous dynamics can be mapped onto a planar flow. Because of the limited set of asymptotic behaviors allowed by flows in  $R^2$  [10] they are particularly easy to classify. Given the fixed points of the flows there is a finite set of possible asymptotic behaviors and transitions among them [11]. Thus, we can classify *families* of planar flows that smoothly deform into one another by varying parameters [12]. It is important to note that this is a *global* description, as opposed to the local one provided by near threshold normal forms. This global description is valid for the spatially uniform dynamics. When diffusion terms are added the planar system becomes high-dimensional. We conjecture that there exists a natural global description for the high-dimensional reaction–diffusion system that is the direct analogue of the known global description of the two-dimensional planar system. This means there should exist a *model family* of two coupled reaction–diffusion equations which displays the same patterns and transitions among them as any other member of the class. The central statement is that, for reaction–diffusion systems which in the homogeneous limit can be described by planar flows, these model families are mainly determined by the homogeneous dynamics.

Given a set of two reaction–diffusion equations with bounded diffusion terms, the local dynamics at each time and point in space is, properly understood, a perturbation of the homogeneous planar flow. Thus, the model family of the class which a particular system belongs to

should not only display homogeneous behaviors that are topologically equivalent to those of the system we are trying to classify, but it should also contain its closest perturbations. Since flows in  $R^2$  with a finite number of fixed points have a finite set of asymptotic behaviors and can undergo a countable set of bifurcations, we then expect to find a countable set of model families. This gives the desired classification of excitable systems describable by pairs of reaction–diffusion equations. In this Letter we present a particular application which supports our viewpoint.

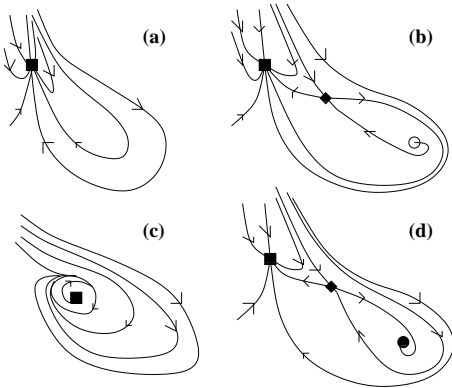


FIG. 1. Planar flow with one excitable fixed point (a) and its closest perturbations (b)–(d).

We first develop a simple geometric model of excitability in  $R^2$  suitable for our purposes. We consider a set of equations  $\dot{u} = f(u, v)$ ,  $\dot{v} = g(u, v)$ , with only one attractor: a stable fixed point,  $\bar{x} \equiv (\bar{u}, \bar{v})$ . Excitability implies that the flow lines turn around before coming back to  $\bar{x}$ . The simplest situation with this property is depicted in Fig. 1 (a), that corresponds to the case in which  $\bar{x}$  (the square) is the only limit set of the flow. This flow can generically undergo a “saddle–repellor”, a saddle–node or a Hopf bifurcation, leading to the flows shown in Figs. 1 (b)–(d), respectively. The fixed point  $\bar{x}$  is stable in all cases but in (d), where there is an attracting limit cycle. In Fig. 1 (b) and (c) it coexists with a saddle (the diamond) and a repellor (the white circle) or a node (the black circle). While the Hopf bifurcation requires that  $\bar{x}$  be a spiral, which is unrelated to it being excitable, the saddle–node and saddle–repellor bifurcations may be linked to the excitability of  $\bar{x}$ . In fact, excitability is related to the existence of a separatrix, which becomes the stable manifold of the saddle after it is born. Also, the turn around of the flow lines implies that the orientation of the *nullclines* (the curves that satisfy  $f(u, v) = 0 = g(u, v)$ ) is such that, by not too large a perturbation, they can eventually become tangent at a point. Generically, when this happens, a saddle–node or saddle–repellor bifurcation occurs. These two types of bifurcations “meet” at a codimension two point, the Takens–Bogdanov point. In fact, the simplest family that contains the flows in Figs. 1 (a)–(c) outside a

neighborhood of  $\bar{x}$  is given by the Takens–Bogdanov normal form [13]:  $\dot{u} = v$ ,  $\dot{v} = \mu_1 + \mu_2 v + u^2 + uv$ . It is easy to modify these equations so that they also describe the behavior at and near  $\bar{x}$  (see *e.g.* [9]). Flows of this “extended” family with only one fixed point have the inflection of the flow lines necessary for excitability. We may thus call it a general model of excitability in  $R^2$ , for systems with one fixed point. Since the family contains all the relevant perturbations of the flow in Fig. 1 (a), it is also suitable in the extended case [14].

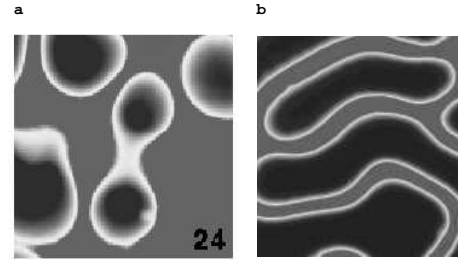


FIG. 2. Transition from replicating spots to labyrinthine patterns in the FIS reaction when the homogeneous system approaches the saddle–node saddle–repellor bifurcation.

We now consider a reaction–diffusion system with an underlying planar homogeneous dynamics that has only one stable but excitable fixed point. As a model family of its class we choose a two–variable reaction–diffusion system that, in the homogeneous limit, contains the flows in Figs. 1 (a)–(c). Now, any affine transformation  $(u, v) \rightarrow \mathcal{M}(u - u_0, v - v_0)$ , with  $\mathcal{M}$  a constant  $2 \times 2$  matrix, will give another family with an equivalent homogeneous dynamics and, in many cases, the right “winding” of the flow lines. If we introduce such a transformation in the set  $\partial_t u = D_u \nabla^2 u + f(u, v)$ ,  $\partial_t v = D_v \nabla^2 v + g(u, v)$ , we get a new set with cross–diffusion terms. Thus, once we have any family,  $\dot{u} = f(u, v)$ ,  $\dot{v} = g(u, v)$ , with the “right” homogeneous dynamics, we expect, in most cases, that each (stationary) pattern of the system of interest be equivalent to a pattern of a flow in the family

$$\begin{aligned} \partial_t u &= D_{uu} \nabla^2 u + D_{uv} \nabla^2 v + f(u, v), \\ \partial_t v &= D_{vu} \nabla^2 u + D_{vv} \nabla^2 v + g(u, v). \end{aligned} \quad (1)$$

Since it is possible to get rid of cross–diffusion by a simple transformation, it should always be possible to choose a *particular* model family without it.

Now we discuss three concrete examples of systems with the excitable homogeneous dynamics discussed above. Consider the FIS reaction, which produces the patterns of Fig. 2 [3]. In the well–mixed (*i.e.*, spatially homogeneous) case, it is known to exhibit excitability, bistability and oscillations [15]. These homogeneous behaviors can be described by planar dynamical systems. The dynamical models of the system (a set of 10 ODE’s) [16] show that for the parameter values used in all the experiments, there is a separation of timescales

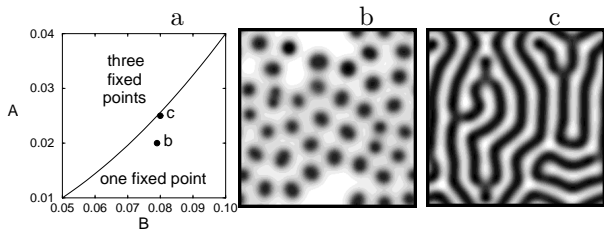


FIG. 3. A partial bifurcation set for the homogeneous Gray-Scott model (a) and two examples of patterns that occur for the parameters indicated in (a) when  $D_u = 1$  and  $D_v = 0.5$ . The line corresponds to the curve of saddle-repeller bifurcations.

that allows the reduction of the original 10-dimensional system to a planar one. This planar system can have at most three fixed points, one of them a saddle. Experimentally, only stable solutions can be observed. The existence of the unstable fixed points and other limit sets are deduced from the model.

In this Letter we discuss the replicating spots (Fig. 2 (a)) and lamellar structures (Fig. 2 (b)) that are found when there is only one homogeneous stationary solution, the low pH fixed point, and it is stable [3]. Experimentally, the spots are initiated by finite perturbations of the low pH state. This reflects its excitability. Thus, a model family like the one sketched before should reproduce at least some of the observed patterns. The transition from spots to lamellae shown in Fig. 2 is observed as the concentration of ferrocyanide,  $[\text{Fe}(\text{CN})_6^{4-}]$ , is decreased [3]. The homogeneous system approaches a saddle-node bifurcation as  $[\text{Fe}(\text{CN})_6^{4-}]$  is decreased. Below a critical value there are three fixed points (a low pH one, a high pH one, and an intermediate pH saddle). Above this value only the low pH fixed point persists. We will show that both the patterns and this transition are contained in the model family we propose.

The Gray-Scott and Fitzhugh-Nagumo models display spot replication and lamellar patterns. The Gray-Scott model is given by [4], [17]:

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_u \nabla^2 u - uv^2 + A(1 - u), \\ \frac{\partial v}{\partial t} &= D_v \nabla^2 v + uv^2 - Bv,\end{aligned}\quad (2)$$

and it has been shown to behave similarly to the experiment [3]. The Fitzhugh-Nagumo model [18], [5], can be written as:

$$\begin{aligned}\frac{\partial u}{\partial t} &= D_u \nabla^2 u - \alpha(v + a_1 u - a_0), \\ \frac{\partial v}{\partial t} &= D_v \nabla^2 v + v - v^3 + u.\end{aligned}\quad (3)$$

The homogeneous dynamics of both models is a flow in  $R^2$ . Furthermore, the families described by Eqs. (2) and (3) contain the flows of Figs. 1 (a)–(c). Thus, both systems have the “right” homogeneous dynamics to

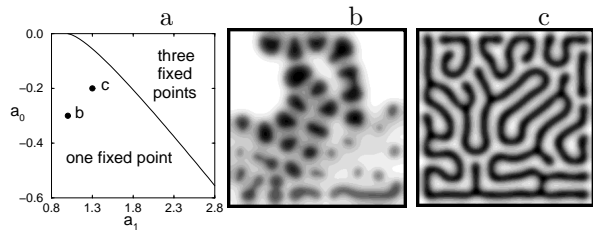


FIG. 4. Similar to Fig. 3, but for the Fitzhugh-Nagumo model. The examples in (b) and (c) were obtained for  $D_u = 1$  and  $D_v = 0.166$ .

construct model families of one another and of the FIS reaction. We conclude that all these systems belong to the same equivalence class. Furthermore, for the qualitative comparison we present, cross diffusion terms are not necessary and either Eqs. (2) or (3) can be used as the model family for this class.

We show in Figs. 3 and 4 snapshots of some of the patterns obtained in numerical simulations of Eqs. (2) and (3), respectively, when the systems have only one stable but excitable fixed point. We observe spot replication and labyrinthine patterns. As in the experimental system, we observe a transition from spots to lamellar patterns as the homogeneous systems approach the saddle-node (saddle-repeller) bifurcation (see the partial bifurcation sets shown in Figs. 3 (a) and 4 (a)) [19]. We can provide a rough explanation for this if we think of stationary solutions and regard diffusion as a perturbation on the homogeneous dynamics at each spatial point. In this sense, diffusion makes the system cross the saddle-node (or saddle-repeller) bifurcation. It is clear that the closer the homogeneous system is to the bifurcation, the smaller must be the perturbation and thus  $\nabla^2 u$  and  $\nabla^2 v$ . For this reason, more spatially extended patterns with smaller Laplacians (such as lamellae) can be supported when the homogeneous system is closer to the bifurcation point.

We have proposed a global classification scheme for excitable reaction-diffusion systems in terms of model families whose choice is based on their underlying homogeneous dynamics. We have concluded that the FIS reaction and Eqs. (2) and (3), in the region of parameter space discussed, belong to the same equivalence class. This class is organized around a Takens-Bogdanov point [20] and we call it the *Takens-Bogdanov model of excitability*. Families with other types of homogeneous dynamics will serve as templates for other classes of excitable systems. We believe that this classification approach will be possible whenever the homogeneous dynamics can be mapped onto a planar flow. The fact that limit sets of planar flows are so restricted may be the explanation of the ubiquitous presence of certain patterns in diverse systems. For example, this might be the reason that the complex Ginzburg-Landau equation reproduces behaviors outside its range of applicability as a near-threshold normal form.

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